Protodrilus gelderi, a new species of infralittoral, interstitial polychaete from Massachusetts Bay

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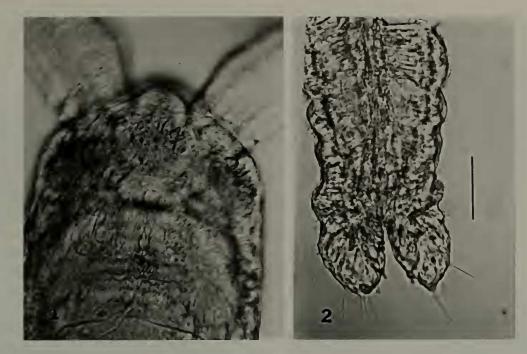
Abstract.—A new species of the interstitial meiofaunal polychaete genus *Protodrilus (P. gelderi)* is described from relatively stable, subtidal, shelly substrate that occurs in patches along the north shore of Massachusetts Bay, U.S.A. Males and females differ in total body length as well as in the distribution of salivary glands and gamete producing regions of the body. With the exception of the absence of segmentally arranged ciliated bands, males of the new species are morphologically quite similar to *P. ciliatus*. However, the females differ markedly from all previously described species in that the ovaries are present from the first segment to the posterior end of the body.

Interstitial meiofaunal polychaetes have commonly been encountered in coarse shelly substrate collected by divers at shallow depths in Massachusetts Bay. Polygordius appendiculatus Fraipont, 1887, P. lacteus (Schneider, 1868), and P. triestinus Hempelmann, 1906 are routinely present in large numbers in such substrate at depths of 3-30 m. In some of these samples from Nahant Bay and Broad Sound at depths of 6-20 m, a previously undescribed species belonging to the genus Protodrilus, usually numbering in excess of 50 per 8 ounce (volume) plastic bag of substrate, has also been present. Other species of Protodrilus have been encountered during intertidal meiofaunal studies along the shores of the Gulf of Maine, but this species appears to be strictly subtidal. Ruebush (1939) reported Protodrilus leuckarti Hatschek, 1880 from specimens collected intertidally by Dr. Donald Zinn at Branford, Connecticut, USA. No further details were presented in the paper; however, Jouin (1970) stated that it was more likely that the specimens were P. ciliatus Jägersten, 1952 and this unconfirmed report remains the only record of a species of the genus in New England. The following description of the new species from the subtidal is derived primarily from living specimens.

Materials and Methods

Substrate was collected by Scuba divers using garden trowels or large Modiolus shells for scooping into plastic bags. The bagged samples were maintained in the laboratory on a running seawater table to prevent temperature shock prior to sorting. The sediment was extracted with 7.5% MgCl₂, and decanted onto 153 µm screens from which the animals were washed into shallow dishes containing fresh sea water. More than 200 living individuals have been examined since the species was first encountered in 1976 in an effort to determine distribution of nephridia and location of sperm ducts. Weather conditions have prevented collecting between February and April. Stabilization of substrate following winter storms has necessitated an annual search to relocate areas occupied by animals of interest. The new species has only been obtained between June and January during which time, small and sexually immature specimens have been uncommon.

Anesthetized specimens were fixed in Hollande's cupri-picri-formal-acetic and



Figs. 1, 2. *Protodrilus gelderi*, living specimens. 1. Dorsal view of anterior prostomial region. 2. Caudal lobes, scale =0.08 mm.

whole mounts were stained with Mayer's alcoholic HCl carmine, in some instances counterstained with indigo-carmine. Suitable fixed individuals were selected for sectioning following embedding in Steedman's polyester wax. Mounted sections were treated and subsequently stained with Heidenhain's Azan or Alcian blue buffered to pH 2.5 (Humason 1967).

Family Protodrilidae Czerniavsky, 1881 Protodrilus gelderi, new species Figs. 1–8

Type specimens.—Zoologisches Museum der Universität Hamburg: holotype female P-23532 and allotype male P-23533, whole mounts on one slide. Muséum National d'Histoire Naturelle de Paris: paratype male UE 622, female UE 623. American Museum of Natural History: paratype male AMNH 4194, female AMNH 4193. U. S. National Museum of Natural History: paratype male USNM 175429, Female USNM 175428.

Type locality.—Coarse shelly sand, off north side of Egg Rock, 20 m depth. Nahant Bay, MA., 42°26'N; 70°54'W.

Description.-Body slightly transparent;

red coloration associated with buccal mass; gut green to brown. Up to 44 segments in mature individuals, females to 9 mm in length and males to 7 mm. Head broader than following region of body; midbody slightly broader than head, tapering to posterior end. Caudal lobes broad, fan-shaped, with four or more large stereocilia (Fig. 2) projecting from posterior margin. Prostomium bluntly rounded with four stereocilia around apex. Tentacles up to 1.2 mm long, extending back to segment 6. Ocelli absent. Pair of anterior sensory organs ("statocysts") $\sim 16 \ \mu m$ diameter to either side of prostomial apex. Nuchal organs large, slitlike, and lateral, at bases of tentacles. A single very long stereocilium about half head diameter, on dorsal surface immediately behind top of each nuchal organ. Small, ciliary patches present on head and body, ciliary annulations absent. A stereocilium is present laterally near the anterior and posterior end of each segment, and one is sometimes present in the middle of the lateral margin. Curved (gourd shaped) bacillary gland cells $\sim 30 \ \mu m$ long and 7 μm maximum diameter, in thick double row across head behind nuchal organs, scattered

in epidermis of anterior body segments becoming more abundant posteriorly, concentrated along sides of ventral ciliated furrow. Pygidial stylus not evident. Salivary glands extend into segment 12 in most males, to 19 maximum; at least into segment 15 and up to 30 in females. Ovaries occur from segment 1 or 2 into penultimate or antepenultimate segment. Oviducts and dorsal organs absent. Testes from segment 11 to antepenultimate segment. Male lateral organ in segment 7, large, round, surrounded by gland cells, followed by a continuous ciliated furrow from segment 8 to 17–18; spermducts in 12 through 15.

Etymology.—The species is dedicated to Dr. Stuart R. Gelder who as a predoctoral student carried out part of his dissertation investigations at our laboratory and introduced me to histochemical procedures which could be applied to the study of interstitial polychaetes.

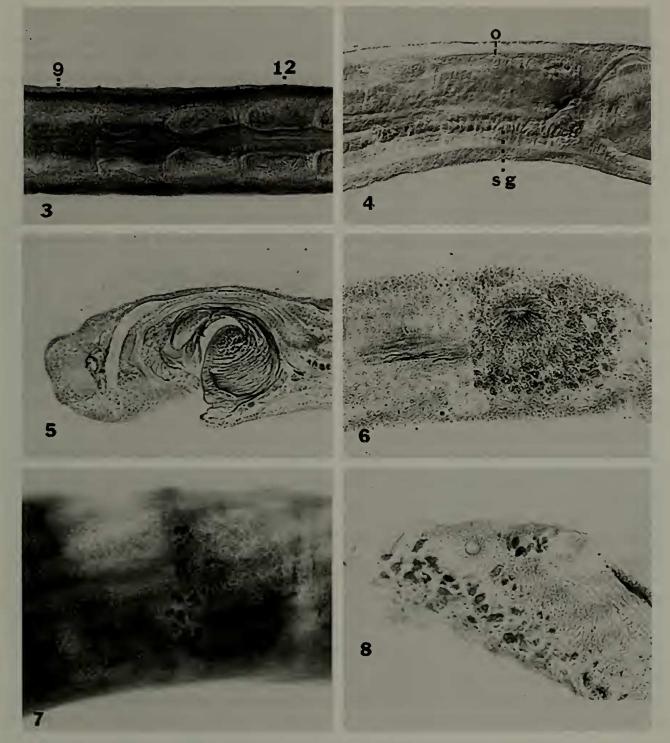
Observations.—Total length and number of segments of mature animals are variable features frequently attributable to posterior regeneration. The anterior sensory organs contain an amorphous body and are not readily visible. In sections, these bodies appear as a gel, but in whole mounts are divided into two or three parts. The large, lateral, slit-like nuchal organs are the only obvious area on the head bearing motile cilia, as the cilia tufts on the head are insignificant. SEM indicates that the stereocilia on each body segment are arranged in three interrupted rings. A row of pigment cells extends across the prostomium (Fig. 1) immediately behind the nuchal organs. The bacilliary gland cells stain strongly with Alcian blue pH 2.5, and are cyanophilous with Azan. In sections, it can be seen that the cell bodies displace the other epidermal cells and bulge beneath them, so that the epidermis could be described as pseudostratified. They can be distinguished by their rods from other mucous cells which also expand beneath the surficial epidermal cells. Mucous cells are abundant in and along the sulcus between segments, and are

dominant (Figs. 6, 8) outside the layer of serous cells which discharge into the lateral organ in segment 7 of the males. These serous cells are also subepidermal with long necks which pass between the ciliated support cells of the organ (Fig. 6). Parenchyme cells fill the area, laterally, between the epidermis and longitudinal muscles. However, the cells are absent near the middorsal and midventral lines of the body. There are usually nine diagonal muscle bundles on either side in each segment of mature individuals. Salensky (1907) stated "ungefähr 6-7" in the Protodrilus species which he investigated, noting that the number was much smaller than in the genus Polygordius. The arrangement of these muscles in sectioned material is similar to the diagram by Pierantoni (1908: pl. 2, fig. 2). Relaxation of these muscles allows a flattening of the body, and expansion of the ventral ciliated creeping groove.

The strong retractor muscles of the buccal mass usually contract following fixation, so that the esophagus is arched as it passes over the mass (Fig. 5) to open at the anterior margin of the mouth. As a result, the initial group of salivary glands are drawn forward along the sides of the arch. In living individuals, the base of the esophagus is a straight tube extending back from the arched portion. The epithelium of the esophagus is initially composed of tall, thin, simple columnar cells with long cilia (Fig. 5). The longest region is formed by cuboidal cells with relatively large roundish nuclei, and the cilia are spread apart. This is possibly an artifact resulting from the stretching of this region, although there is no intergradation (Fig. 5) with the cells of the anterior or posterior regions. The posterior straight part of the esophagus is lined with very tall ciliated columnar cells which are closely packed together.

Variation in the number of segments containing salivary glands may be the result of posterior regeneration and is most noticeable in females. The number of salivary gland cells is reduced, often to one or two,

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Figs. 3–8. *Protodrilus gelderi*, segments 9–13 of male; dorsal view, whole mount, Mayer's carmine with indigo carmine counterstain. 4. Anterior segments behind buccal mass of holotype female; ovaries (o) of right side in focus, sg = salivary glands, Mayer's carmine. 5. Longitudinal section through esophageal region; Azan stain. 6. Slightly oblique section through aperture of male organ in segment 7; Azan stain. 7. Male organ in segment 7 with longitudinal trough extending posteriorly from it; whole mount, Mayer's carmine with indigo carmine counterstain. 8. Oblique section through aperture of male organ. Alcian blue pH 2.5 stain.

along each side of the midgut of the last few segments in which they occur.

The pair of testes in segment 11 (Fig. 3) have rarely contained spermiogenetic stages. The male lateral organ in segment 7 is large and obvious as is the ciliated furrow which begins immediately behind it (Fig. 7). The sulcus between segments 7 and 8 is densely ciliated with closely packed mucous cells. Only euspermatozoa have been observed.

The first pair of ovaries in preserved

specimens, frequently project forward against the buccal cavity as the result of the retraction of the buccal mass drawing the esophagus and initial salivary glands up over it. The first two pairs of ovaries are smaller than subsequent ones and contain fewer oocytes. They are often difficult to observe in cleared, preserved specimens and whole mounts (Fig. 4). Oocytes are small, attaining a diameter of ~25 μ m with large germinal vesicles. There are slightly over 50 oocytes in each mature pair of ovaries. Maturation of ovaries is sequential with the smaller, less mature ovaries anterior and posterior to the mid-body region.

The only ciliary action observed in the body cavity has come from a large pair of metanephridia in segment 8 of both sexes. The metanephridia are located on each side in this segment, and they appear to be the only excretory organs in the body.

Protodrilus gelderi either attaches to the substrate with its caudal lobes or swims upward with a violent wriggling motion when disturbed, an escape strategy that was reported in the description of *Protodrilus albicans* Jouin, 1970. Specimens maintained in the laboratory are most frequently encountered on the sides of the bowls or gliding on the surface film. Individuals live for several weeks in finger bowls of clean sea water at approximately ambient sea temperature, but a satisfactory food source has not been discovered to maintain them. Loss of the red pigment around the buccal mass occurs in a few days after isolation.

Discussion

The histology and organology of the genus *Protodrilus* were extensively described by Pierantoni (1906) and Salensky (1907). Differences between species are not apparent at those levels except for the distribution of cell types in the epidermis. However, such variations may be attributable to different environmental conditions or a technic artifact. Gross anatomy of sexually mature individuals shows variation which allows for the identification of living worms, and often from stained whole mounts of well anesthetized individuals. The secondary sexual characters of males have been the most frequently used features to distinguish species. Females tend to be conservative in the degree of variation except for oocyte number and size, and the occurrence of cocoon glands.

The four stereocilia around the apex of the prostomium appear to be a basic character of the genus, and thus, plesiomorphic. Purschke (1990a, 1990b) examined the so called "statocysts" located near the apex of the prostomium of a number of species of Protodrilus. He concluded that they were not statocysts and based upon TEM observations were more likely involved in photoreception. Purschke (1990b) referred to them as anterior sensory organs to distinguish them from the phaosome-like posterior receptors of Protodrilus adherens Jägersten, 1952. They differ from pigmented ocelli, and he postulated that they constituted an autapomorphy for the genus. The opacity of the preoral region of the prostomium of living P. gelderi makes it very difficult to observe them with transmitted light, in spite of their size. The contents of the organelle, which appear as a partitioned gel in histological preparations, apparently are the paracrystalline bodies described from TEM observations by Purschke (1990b).

Protodrilus gelderi differs from other members of the genus in the presence of ovaries along almost the entire length of the female mid-gut. No species has been described previously in which ovaries are present anterior to the segment 7, or with salivary glands in females posterior to segment 20. Pierantoni (1906, 1908) noted that Uljanin (1877) and Hatschek (1880) had identified the salivary glands as ovaries, and they had concluded that the species of *Protodrilus* which they had described were hermaphroditic based upon the subsequent posterior occurrence of testes in the same specimens.

Males are morphologically similar to those of P. ciliatus, differing primarily in the absence of ciliary annulations. Among species lacking such annulations, they are similar to Protodrilus submersus von Nordheim, 1989 and P. albicans, in both of which, however, salivary glands are absent from the fertile region. Bacillary glands are densely packed in the dorsal epidermis, and nephridia are readily apparent in all segments of living P. submersus (pers. obs.) in contrast to the situation in P. gelderi. Protodrilus albicans is described as much larger than P. gelderi and is figured with oval, dorsal nuchal organs. Jouin (1970) did not mention pigmentation of the buccal mass for P. albicans, although she recorded it's presence for other species described in the same paper. The implication was that the mass was not pigmented.

Acknowledgments

Intertidal interstitial faunal investigations over the past thirty-five years have been extended into the subtidal by the cooperation of many students who, while diving to do their thesis research, carried plastic bags to obtain "any coarse sand" they might encounter. Their willingness to help is sincerely appreciated. This paper represents Contribution No. 224 from the Marine Science Center of Northeastern University.

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